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The Morphology of the Esophageal First Instar Larvae of Hypoderma Lineatum Devillers

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THE MORPHOLOGY OF THE ESOPHAGEAL FIRST INSTAR LARVA

OF *HYPODERMA LINEATUM* DEVILLERS

By

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This thesis is approved as a creditable, independent investigation by a candidate for the degree, Master of Science, and acceptable as meeting the thesis requirements for this degree; but without implying that the conclusions reached by the candidate are necessarily the conclusions of the major department.

CONTENTS

INTRODUCTION

During the life cycle of Hypoderma lineatum DeVillers, the first instar larva spends considerable time migrating through the body of the host. During this migration the larva spends a period in the submucosa of the esophagus. This stage is referred to as the esophageal first instar. The following study was conducted on cattle grubs of this stage.

The larvae which were used in this study were dissected from beef gullets obtained from the John Morrell & Company Packing Plant. The gullets were used in a South Dakota Experiment Station project involving the experimental control of these larvae.

PREVIOUS WORK

Very little material is available on the anatomy or morphology of H. lineatum larvae. Ono (4), in 1932, published an account on the morphology of this species of maggot. His study was made on live specimens and does not go into much detail on the internal structure.

Several morphological studies have been made on other dipterous larvae whose morphology appears to be similar in some respects to H. lineatum. Some of these are Lowne's (3) study of the blow-fly made in 1890-92, the study of the apple maggot by Snodgrass (6) in 1924 and the study of the housefly by Hewitt in 1914 which was reviewed by West (9) in 1951.

TECHNIQUE

A general study of the internal organs of the first instar cattle grub is possible without dissection due to the transparent nature of the integument. For closer and more detailed study, however, it is necessary to make slides of serial sections. This was accomplished as follows:

Fixing

Two fixing reagents were used in this histological work. They were made up according to the following formulae:

1. FAA - - - - - - - - - - -	70 percent alcohol - 90 cc
	Commercial formalin - 10 cc
	Glacial acetic acid - 2 cc
2. Petrunkevitch's paranitro-phenol 20% formalin	60 percent alcohol - 100 cc
	Nitric acid c.p. - 3 cc
	Ether - - - - - - - - 5 cc
	Cupric nitrate c.p. 2 grams
	Paranitro-phenol c.p. 5 grams
	Formalin (reagent) - 12 cc
	(formalin added just before use)

In all cases where FAA was used as a fixing reagent the specimens remained in the fixative for six to eight hours. When Petrunkevitch's fluid was used, the specimens remained in the fixative for 24 hours.

Dehydrating

An ascending series of alcohol from 70 percent to absolute alcohol was used in dehydrating specimens fixed in either of the fixatives. The larvae remained in each of the alcohols for a period of one hour.

Clearing

Xylol and dioxan were both used as clearing reagents. The specimens were transferred from the absolute alcohol to a mixture of absolute alcohol-50% and clearing fluid-50%. They were left in this solution for one-half hour. Those specimens that were cleared in xylol remained in the pure xylol for one-half hour and those cleared in dioxan were taken through two changes of pure dioxan, remaining in each for one hour.

Infiltrating

A product of the Fisher Scientific Company called "Fisher tissuemat" was used in place of paraffin for infiltrating and embedding. The "Fisher tissuemat" is a rubber-paraffin combination which in this case had a melting point of 54 to 56°C.

The larvae were taken from the clearing reagent and placed in a saturated mixture of the clearing reagent and "tissuemat". They remained in this solution for one-half hour. Following this the larvae were immersed in three consecutive baths of pure "tissuemat". The grubs remained for one hour in each bath.

Embedding

The melted "tissuemat" from the third bath was used for embedding.

The sectioning was done at 15 and 50 microns.

The slides that were to be used for mounting sections of the larvae were washed for a minimum of four hours in K_2CrO_4- H_2SO_4. They were then rinsed in distilled water and stored in acetone until they were to be used.

In affixing the sections to the slides the following procedure was used: the slides were removed from the acetone and allowed to dry. A thin film of Mayer's albumen was then spread over the surface of the slide and following this several drops of a solution containing three drops of Mayer's albumen in 30 cc of distilled water was placed on the slide. The sections were then floated on the slide and the slide was placed on a heating plate until the water was evaporated.

The staining was done with Harris's Hematoxylin. Balsam was used as the mounting medium.

Whole mounts were stained by following Lynch's precipitated Borax-carmine method (2).

DIFFICULTIES ENCOUNTERED

The cuticle of the larva tended to shrivel and change to a silvery white color in the technique used as described. This would happen when the specimen was in the clearing agent or in the saturated solution of the clearing agent and the "tissuemat". An occasional specimen, however, would come through this process unchanged and appear normal. Attempts were made to shorten the process of dehydration by passing the specimens from 70 percent alcohol into dioxan, but here again the specimens were not usable.

Upon sectioning the occasional specimen which appeared normal, as referred to above, the mid-gut was found to be too hard and very few usable sections could be obtained. Several methods were tried in an attempt to overcome this difficulty. Some grubs were injected with the fixing fluid a short time after they were placed in the fixative. In other cases small incisions were made through the cuticle to allow a freer movement of the reagent into the body. In neither case was it possible to obtain satisfactory sections from this material. Finally either the anterior or the posterior one-third of the body was cut off; this allowed a free movement of the reagent into the mid-gut. Apparently the latter technique overcame the difficulty as usable sections resulted. Cutting of the body was done after the specimen was fixed to the extent that the body fluids would not drain out. It was necessary to make the cut so as to remove a portion of the mid-gut and thus directly expose its interior. Possibly the same results could be obtained by making an incision through the integument and the wall of the mid-gut.

The use of stained whole mounts was not satisfactory for the cuticle had a tendency to fold, thus making difficult the actual study of the internal organs.

GENERAL EXTERNAL ANATOMY

The first instar larva taken from the esophagus of cattle is somewhat cigar shaped. The anterior part of the body is more tapered than the bluntly rounded posterior end. The body wall is transparent and colorless. The mouth hooks are located on the extreme anterior portion of the body. The posterior spiracles are on the rather blunt posterior end. The posterior half of the last segment bears numerous dark spicules which can be seen with the naked eye.

The larvae used were from six to fifteen millimeters in length. The body is composed of eleven discernible segments.

INTEGUMENT

The body wall or cuticle of the esophageal stage larva is made up of two obvious layers, the epicuticula and the endocuticula. The epicuticula appears as a narrow clear outer covering. The remainder of the cuticle or endocuticula is for the most part similar throughout. However, in some instances, with close study, a slightly discernible differentiation can be seen between the outer portion of the endocuticula (the exocuticula) and the remainder of the endocuticula (Pl. 1, Fig. 1). This differentiation in the endocuticula is largely a matter of color and is due, according to Snodgrass (7), to a greater degree of sclerotization in the outer portion. This portion he calls the exocuticula. Richards (5) stresses the point that the cuticle is an entity and has no distinct abrupt differentiation marking the divisions.

Beneath the cuticle and adhering to its inner surface is a single layer of flattened hexagonal cells which make up the epidermis (Epd Pl. 1, Fig. 1; Pl. 1, Fig. 2). The nuclei of the epidermal cells are large and stain heavily.

The outer surface of the cuticle bears small noncellular cuticular processes which will be called spicules in this work. There are three types of spicules. One type is a very minute wedge-shaped spicule (Pl. 1, Fig. 3), whereas the other two types are cylindrical and somewhat curved (Pl. 1, Fig. 4).

The minute wedge-shaped spicules are found on all but the posterior segment. Sadao Ono (4) states that the very minute spicules are arranged in a few rows anteriorly on the ventral and dorsal sides of each of the first nine segments, and are scarcely detectable on the ventral side of the tenth segment. However, the writer found these spicules over the entire surface of segments one through nine, but they were more numerous on the anterior portion of the segments.

The spicules of the eleventh segment are confined to its posterior portion. These are of the cylindrical, slightly curved form. One type is large and can be seen as a black spot with the naked eye. This spicule has an elevated sclerotized base. The other type is smaller and lacks the sclerotized base (Pl. 1, Fig. 4).

All the spicules are sclerotized. The minute, wedge-shaped and the minute, cylindrical, curved spicules appear to be attached to the outer surface of the epicuticula, whereas the larger spicules of the eleventh segment have a sclerotized base which extends down through the epicuticula (Pl. 1, Fig. 3 & 4).

There is no apparent differentiation of an intersegmental membrane between segments. There is, however, an infolding of the cuticle between the segments. The inner surface of this intersegmental constriction serves as a region for muscle attachments (Pl. 1, Fig. 6). These presumably are apodemes, though an epidermal layer of cells cannot be seen bordering the full edge of the apodeme. The muscle fibers attach to the apodeme by numerous tonofibrillae which appear to penetrate through the endocuticula (Pl. 1, Fig. 6). An epidermis is not visible underneath the apodeme where it attaches to the endocuticula but a series of short heavy line-like sclerotized markings are present instead (Pl. 1, Fig. 6).

Other muscle attachments can be seen on the wall of the segment (Pl. 1, Fig. 5). These attachments consist of a series of tonofibrillae which anchor the muscle to the cuticle in a manner similar to that described in the preceding paragraph.

MOUTH HOOKS AND PHARYNGEAL SKELETON

The larvae of H. lineatum have the muscoid type of mouth parts which is described by Snodgrass (7) as a type in which "... the usual mouth parts are entirely suppressed in the larval stage and the only external feeding organs of the maggot are a pair of strong mouth hooks movable in a vertical plane".

The mouth hooks of the esophageal first instar larva are in the form of two semilunar structures with the points directed anteriorly, laterally and slightly ventrally (Pl. 2, Fig. 1). On the inner face of each mouth hook is a small tooth-like projection. This tooth is located about one-fourth to one-third of the way back from the anterior point (th Pl. 2, Fig. 1). Each mouth hook is articulated on the end of a heavily sclerotized stalk which extends back and apparently anchors on the lateral plates of the pharyngeal skeleton (A Pl. 2, Fig. 1).

Bishopp, Laake, Brundrett and Wells (1) described the portion here referred to as stalks (A Pl. 2, Fig. 1) as the pharyngeal skeleton. The stalks of the mouth hooks constitute only one pair of the sclerites which make up the pharyngeal skeleton (Pl. 2, Fig. 3). They are the only heavily sclerotized parts of the pharyngeal skeleton, the other sclerites being only lightly sclerotized. Lowne (3) and Von Hennig (8) also consider the stalks as only a part of the pharyngeal skeleton. Lowne refers to this portion of the pharyngeal skeleton of the blow-fly larva as the hypostomal sclerite.

Between the stalks of the mouth hooks and mesad to their anterior ends is a short, more lightly sclerotized, peg-like body. This portion of the mouth armature is not anchored to the stalks of the mouth hooks. At its anterior end is a spine-like projection that is directed forward (Sp Pl. 2, Fig. 1).

The true head capsule of this larva is completely retracted within the thorax; thus the layer of epidermal cells which covers the head is in the form of a deep fold in the anterior portion of the larval body. It appears as a sleeve of two layers of epidermal cells surrounding the anterior portion of the stomodaeum. The lateral and ventral plates of the pharyngeal skeleton lie within this fold. These plates do not extend the entire length of the infolded epidermal cells. The epidermal layer adheres closely to the plates of the pharyngeal skeleton (Pl. 2, Fig. 2).

The pharyngeal skeleton consists of two lateral, triangular plates to which the stalks of the mouth hooks are anchored, and a finger-like ventral plate (Pl. 2, Fig. 3). These plates are lightly sclerotized with somewhat heavier sclerotization at the anterior end.

MUSCULAR SYSTEM

There are three muscle layers in the body wall of the larva. These are transverse, oblique and longitudinal layers of muscles (Pl. 3, Fig. 1).

The transverse muscles extend from the dorso-lateral portion of the body wall to the ventro-lateral. They have their attachments either directly to the wall of the segment or on the apodeme at the junction between segments.

The oblique muscles lie internal to the layer of transverse muscles and have their attachments on the apodemes between segments.

There are two groups of longitudinal muscles: a dorsal and a ventral group. These muscles have their attachments on the apodemes between segments.

The muscles themselves are formed of groups of striated strands. Each muscle appears to be independent of neighboring muscles.

DIGESTIVE SYSTEM

The digestive system of the esophageal first instar larva is of a rather simple type, being a practically straight tube running from the anterior to the posterior end of the larval body (Pl. 3, Fig. 2).

On the anterior end of the first segment there is a slight invagination of the body wall, the atrium. The anterior opening of the digestive tube or mouth opening is located in the posterior portion of the atrium.

The pharynx, which originates posterior to the mouth opening, is a short enlarged portion of the stomodaeum. The pharynx extends posteriorly into the second segment.

The esophagus is a narrow, thin walled tube which extends from the pharynx to the ventriculus. The esophagus passes below the cerebral lobes of the central nervous system and between the commissures which connect the dorsal and ventral portions of the central nervous system (Pl. 3, Fig. 4).

Lateral to the esophagus and the anterior end of the ventriculus there is a pair of ellipsoid salivary glands. The salivary glands lie in the posterior part of the third segment and the anterior portion of the fourth segment (Pl. 3, Fig. 2). The walls of the salivary glands are made up of large flat cells.

Attached to each salivary gland is a somewhat coiled, narrow salivary duct which extends anteriorly. The two ducts join ventral to the esophagus about half way between the glands and the pharynx. From here a single duct extends forward and this opens into the anterior end of the pharynx.

At the junction of the esophagus and the ventriculus there is a valve-like arrangement which is called the stomodeal or cardiac valve. It appears as a short loop of the esophageal wall extending into the ventriculus so as to form a circular lip at the opening into the mid-gut (Car Pl. 3, Fig. 2; Pl. 4, Fig. 1). In stained sections of the grub there is no evidence of a proventriculus. The same is true of whole mounts and live dissections where the mid-gut is in its natural distended condition. When the ventriculus is punctured in an unfixed larva, however, it appears as though the anterior portion of the mid-gut, where the esophagus is attached, is in the form of a proventriculus.

The ventriculus is a large cylindrical tube which is bluntly rounded at the anterior and posterior ends. It extends from the anterior end of the third segment back into the tenth segment. The diameter of the ventriculus is approximately two-thirds the diameter of the grub. The walls are made up of a single layer of epithelial cells consisting of both digestive and regenerative cells (Pl. 4, Fig. 2).

In the tenth segment the ventriculus opens into the much narrower anterior intestine. This opening is on the posterior dorsal portion of the ventriculus. Close to the point where the mid-gut and the anterior end of the hind intestine join are two diverticula, the malpighian tubules. The malpighian tubules, which originate as two branches, in turn branch again forming a series of four small tubes which turn and coil over and around the posterior portion of the ventriculus (Pl. 4, Fig. 3).

The anterior portion of the proctodaeum (the anterior intestine) extends dorsally and anteriorly making a loop over the posterior portion of the ventriculus. This is the only coil in the otherwise straight food tube of this larva. The loop of the anterior intestine extends forward beyond the middle of the ninth segment. From this loop the anterior intestine extends posteriorly into the tenth segment.

In the anterior portion of the tenth segment the proctodaeum enlarges in diameter forming a rectal sac which extends back into the posterior portion of this segment. Here the proctodaeum narrows down into the double walled rectum. The wall of the rectum consists of an inner layer of small cells surrounded by a layer of much larger cells. The rectum extends from the rectal sac to the anal opening. The latter is ventral to the posterior spiracles on the blunt posterior end of the eleventh segment.

NERVOUS SYSTEM

The central nervous system of the esophageal first instar of the common cattle grub appears very similar to that of the larva of the blow-fly as described by Lowne (3). All the ganglia of the ventral nerve cord are grouped together in a single complex center. The primitive ganglia are not evident.

In the posterior portion of the second segment and the anterior portion of the third segment of the body is a pair of cerebral lobes which are connected dorsally. A pair of commissures from the ventral portion of the cerebral lobes connects this portion of the nerve center with the ventral nerve mass. The esophagus passes through the foramen between the commissures and below the connection of the dorsal lobes (Pl. 3, Fig. 4; Pl. 4, Fig. 5).

The cerebral lobes of this nervous system are similar to the supra-esophageal ganglia of a primitive insect. The remainder of the nervous system is greatly modified (Pl. 4, Fig. 4). The commissures are short, thick nerve masses (Pl. 3, Fig. 4; Pl. 4, Fig. 5). The ventral nerve cord is modified into a single nerve mass from which fine paired nerves extend (Pl. 4, Fig. 5).

RESPIRATORY SYSTEM

The posterior spiracles are located on the posterior end of the larva. They are the only apparent openings of the tracheal system.

Surrounding each of the posterior spiracles are two or three sclerotized plates or flattened spicules (Pl. 5, Fig. 1). The spiracles are circular in shape. A dark, yellowish-colored, tube-like structure connects each spiracle with the main tracheal trunk (Pl. 5, Fig. 2). This is presumed to be a cuticular invagination.

A longitudinal tracheal trunk extends anteriorly from each posterior spiracle. This dorsal tracheal trunk lies lateral to the dorsal portion of the food tube (Pl. 5, Fig. 5). It tapers slightly toward the anterior end.

In the tenth segment there is a large branch which connects the two main tracheal trunks. A lateral tracheal connection originates from the connecting trachea and this can be traced forward through several segments (Pl. 5, Fig. 5). The tracheae making up this lateral connection are really branches of the ventral tubes of the main tracheal trunk.

The dorsal tracheal trunks give off two branches, a dorsal and a ventral, in each segment anterior to the tenth segment. Each dorsal branch is short and soon branches into numerous small tracheoles which supply the tissue dorsal to the food tube. Each ventral branch extends some distance down the side of the larva before it branches. The ventral branches supply the tracheal connections to the visceral organs and the body wall.

The tracheae of the larva are surrounded by an external coat of cells. Within this coating is a spiral cuticular intima, the taenidia, which gives the trachea its characteristic appearance (Pl. 5, Fig. 3). This spiral intima is not present in the tracheoles.

FAT TISSUE

A considerable amount of fat tissue can be seen throughout the body of the larva. As shown by Ono (4) there is a concentration of fat tissue in the vicinity of the salivary glands. There is also a considerable amount of fatty tissue posterior to the mid-gut. A thin sheet of fatty tissue can easily be seen at various places along the wall of the ventriculus.

The cells of fat tissue are small at this stage and no globules of fat are evident within them. As stated by Snodgrass (6) "The fat cells are very small in young larvae and at first contain but little fat". Each fat cell is circular and contains a dark staining nucleus.

The cells of the fat tissue are arranged in various patterns, some appear as chains of circular cells, others appear as loose single cells, and still others form sheets one cell thick (Pl. 5, Fig. 4). The fatty tissue along the wall of the ventriculus appears as a sheet of tissue. This sheet is not a continuous covering of the mid-gut but consists of numerous patches of tissue.

CIRCULATORY SYSTEM

A circulatory system was not observed in either the living or the fixed specimens. The fixed specimens were studied both as whole mounts and serial sections.

SUMMARY

The H. lineatum, esophageal first instar larval body is made up of eleven segments. The integument is not sclerotized but rather appears as a transparent covering. There are three types of spicules present: small wedge-shaped ones on the first ten segments; minute cylindrical spicules, and larger cylindrical, elevated spicules on the eleventh segment.

This larva has the typical muscoid type of larval mouth parts. The pharyngeal skeleton is made up of two lateral plates, a ventral plate and two arm-like sclerites upon which the mouth hooks articulate.

There are three apparent muscle layers in the body wall: the transverse, oblique and longitudinal muscles.

The digestive system is rather simple. There is a narrow tubular stomodaeum, a large simple mesenteron and a comparatively short proctodaeum.

The nervous system is highly modified with a single ventral nerve center which is connected by two heavy commissures to the joined cerebral lobes.

The posterior spiracles are the only openings of the tracheal system. From these spiracles a pair of dorsal tracheae extend forward the length of the body. They give off dorsal and ventral branches which in turn branch giving the tracheole connections to the internal organs.

Fat tissue can be found throughout the larval body. The cells of fat tissue do not contain visible fat globules in this stage.

PLATE 1

Fig. 1 - Cross section of Integument
Enct - Endocuticula Epct- Epicuticula
Epd - Epidermis Exot- Exocuticula

Fig. 2 - Cells of the Epidermis

Fig. 3 - Minute spicules as found on the first ten segments

Fig. 4 - Spicules of eleventh segment

Fig. 5 - Muscle attachment on wall of segment

Fig. 6 - Muscle attachment between segments
Ap - Apodeme Ct - Cuticle
Mcl - Muscle Tfbl - Tonofibrillae

PLATE I

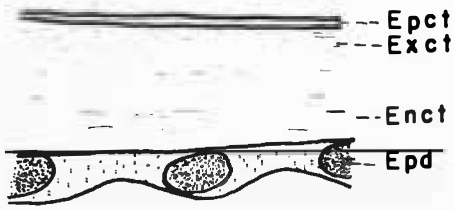


Fig. 1

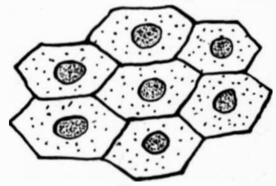


Fig. 2

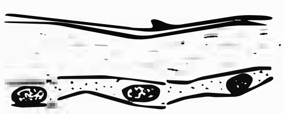


Fig. 3

Fig. 4

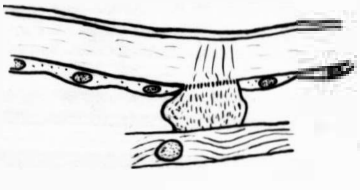


Fig. 5

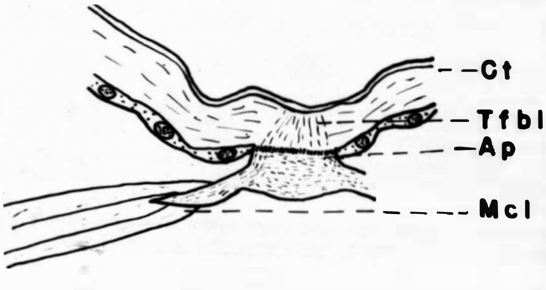


Fig. 6

PLATE 2

Fig. 1 - Mouth Hooks and Stalks
A - Arms of Mouth Hooks
Hk - Semilunar Mouth Hooks
SP - Median Spine
Th - Tooth of Mouth Hooks
X - Point of Articulation

Fig. 2 - Dorsal Cross Section of Pharyngeal Skeleton
A - Arms of Mouth Hooks
B - Lateral Plates of Pharyngeal Skeleton
Epd - Epidermis
Hk - Mouth Hooks

Fig. 3 - Lateral View of Pharyngeal Skeleton
A - Arms of Mouth Hooks
B - Lateral Plates of Pharyngeal Skeleton
C - Ventral Plates of Pharyngeal Skeleton
Hk - Mouth Hooks

PLATE 2

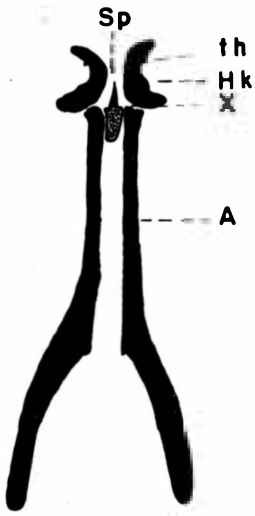


Fig. I

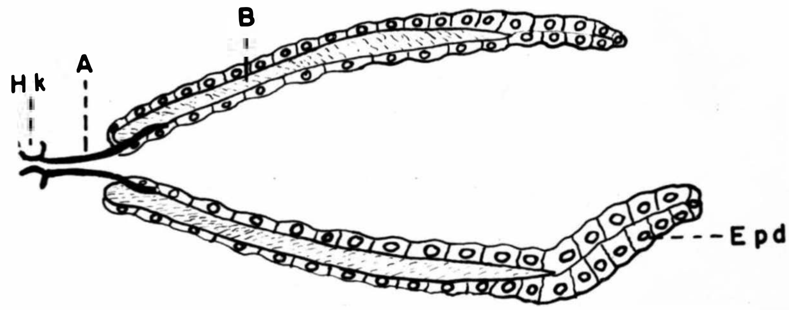


Fig. 2

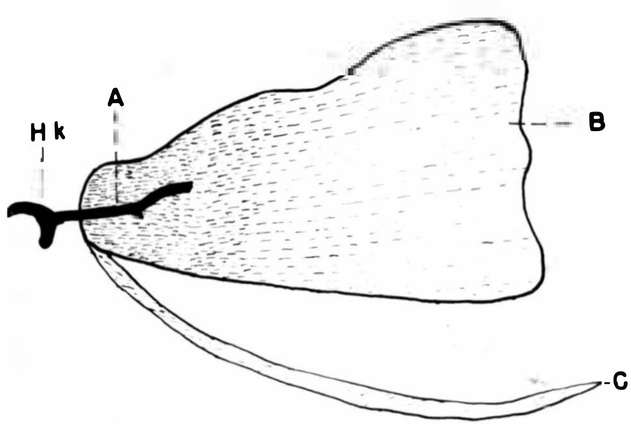


Fig. 3

PLATE 3

Fig. 1 - Musculature of Larva
L Mcl - Longitudinal Muscles
O Mcl - Oblique Muscles
T Mcl - Transverse Muscles

Fig. 2 - Lateral View of Digestive System
A Int - Anterior Intestine
Car - Cardiac Valve
Mal - Malpighian Tubules
Oe - Oesophagus
Phy - Pharynx
Rect - Rectum
R Sc - Rectal Sac
Sl D - Salivary Duct
Sl G - Salivary Gland
Vent - Ventriculus

Fig. 3 - Salivary Gland and Duct
M Sl - Matrix of Salivary Gland
Sl D - Salivary Duct
W Sl - Wall of Salivary Gland

Fig. 4 - Cross Section through Nerve Center
Br - Cerebral Lobes
Cr - Commissures
Oe - Oesophagus
V Nv C - Ventral Nerve Center

PLATE 3

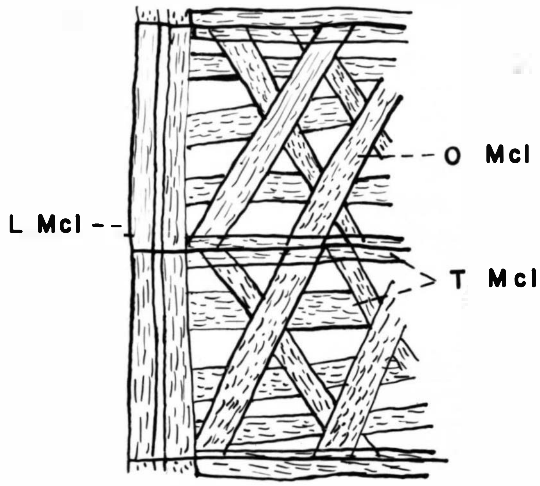
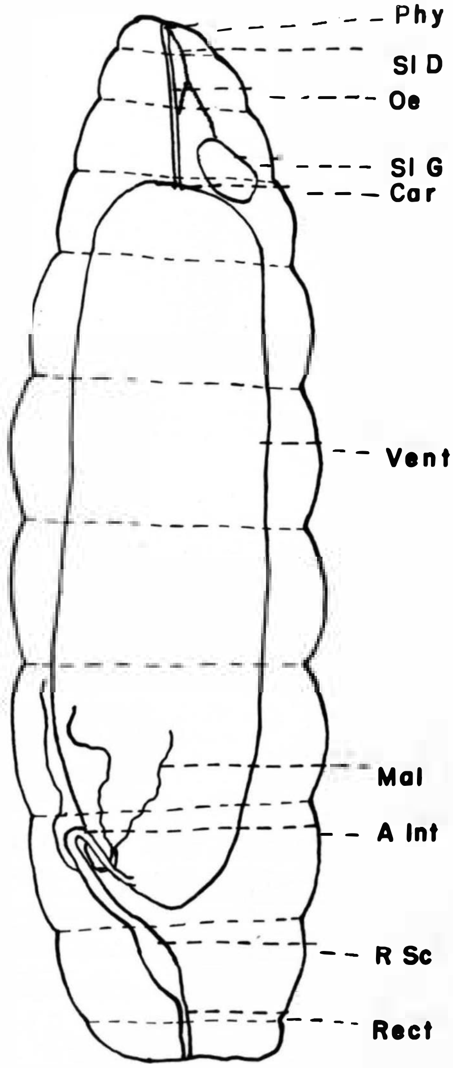


Fig. 1



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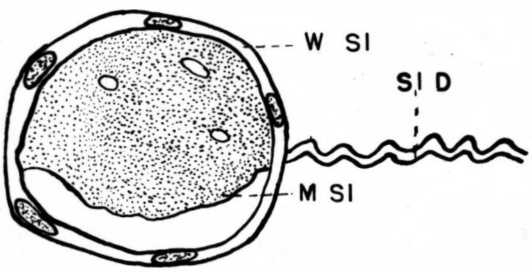


Fig. 3

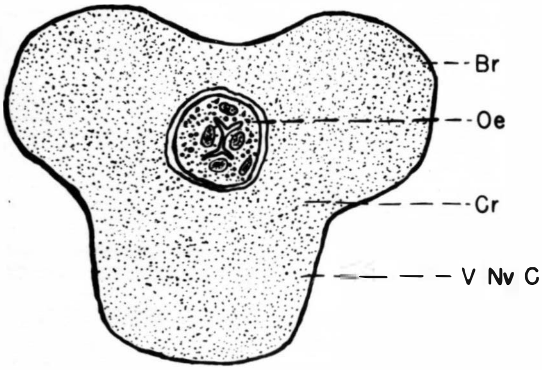


Fig. 4

PLATE 4

Fig. 1 - Cardiac & Stomodeal Valve
Car - Cardiac Valve
Oe - Oesophagus
Vent - Wall of Ventriculus

Fig. 2 - Cells of Wall of Ventriculus

Fig. 3 - Malpighian Tubules
A Int - Anterior Intestine
Mal - Malpighian Tubules

Fig. 4 - Dorsal View of Nerve Center
Br - Cerebral Lobes
Oe - Oesophagus
Vent - Ventriculus
V Nv C - Ventral Nerve Center

Fig. 5 - Lateral View of Nerve Center
Br - Cerebral Lobes
Com - Commissures
Nv - Paired Nerves
Oe - Oesophagus
V Nv C - Ventral Nerve Center

PLATE 4

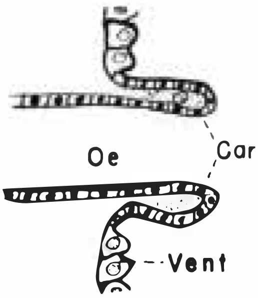


Fig. 1

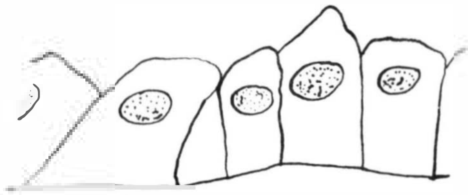
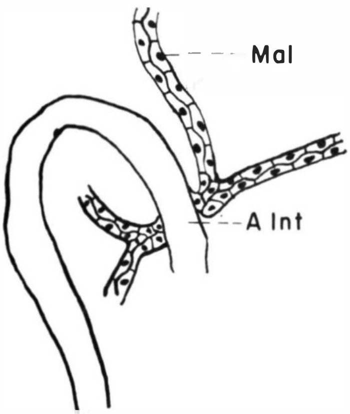


Fig. 2



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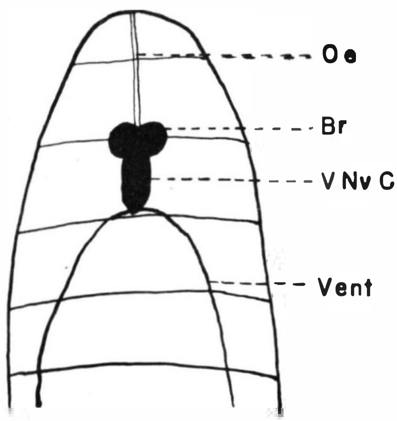

Fig. 4

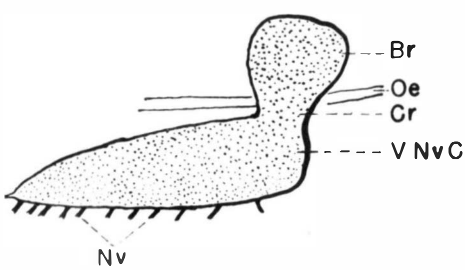

Fig. 5

PLATE 5

Fig. 1 - Posterior View of Posterior Spiracles
Scl - Sclerites
Sp - Spiracles

Fig. 2 - Lateral View of Posterior Spiracles and
Dorsal Trachea
Rect - Rectum
Sp - Spiracle
Tra - Trachea

Fig. 3 - Portion of Dorsal Trachea and Branch
Epth - Epithelium (Cellular Tracheal Covering)
In - Intima of Trachea

Fig. 4 - Fat Tissue - Chain of Fat Cells and Sheet
of Fat Cells

Fig. 5 - Schematic Drawing of Tracheal System
D B - Dorsal Branch
D Tra - Dorsal Trachea
L Tra - Lateral Tracheal Connection
Sp - Posterior Spiracle
V B - Ventral Branch

PLATE 5

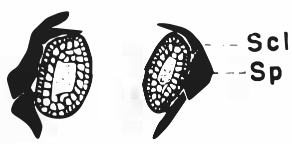

Fig. 1

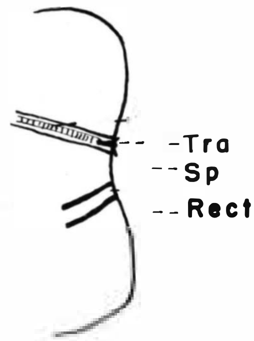

Fig. 2

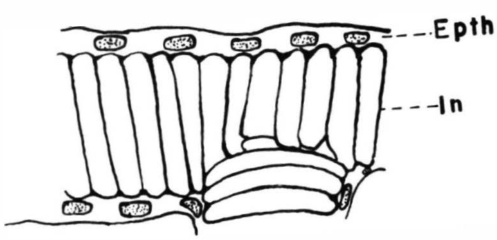

Fig. 3

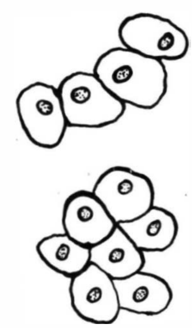

Fig. 4

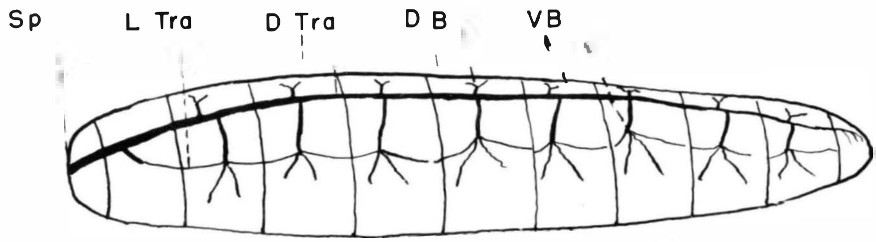

Fig. 5

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